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A study of synapsis and reduction

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(WITH PLATES 12–15)

From the standpoint of heredity the critical stages in an organism are at fertilization and reduction. That in fertilization there is an approximate doubling of the number of chromosomes, half of which were contributed by each gamete, there is no longer any doubt. That this number must be reduced at some time previous to the next union of gametes is equally evident. The method by which reduction is accomplished is not so evident, although the researches of the past few years give promise of an ultimate solution of the problem.

Recent investigations of McClung, Montgomery, Rosenberg, Sutton, Wilson, and others have thrown much light upon the question of the individuality of the chromosomes. The work of these investigators strongly supports the theory that there is a differentiation among the chromosomes. Montgomery ('05) is of the opinion that their individuality is not lost through the growth phase of an organism but that each chromosome of a generation had its predecessor in a preceding generation; that is, there is no *de novo* formation at mitosis. Fick ('05), in a recent discussion in which he goes into the whole cytological question in so far as it bears upon the germ cells, opposes this view as a matter of opinion, but offers no additional data upon the subject. The evidence at present is so very strongly in favor of the theory that the individuality of the chromosomes is retained throughout the history of the organism that it can well be used as a working hypothesis.

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From the time that the first explanation of reduction was offered by Van Beneden, when he believed that half the chromosomes degenerated and were thrown off from the nucleus, until the end of the past century, numerous conflicting views, which need not be reviewed here in detail, were held. It suffices to say that the stimulus to investigation as a result of Weismann's speculations in regard to the chromatin in 1887 produced an immense number of valuable results, some of the most important of which may be mentioned.

Henking ('91) first figured a tetrad, or ring, which he interpreted as a chromosome undergoing one transverse and one longitudinal division, thus giving a true reduction division required by Weismann's theory. Later tetrads receiving the same interpretation were found in animals by Haecker ('95*a*), Paulmier ('99), Ruckert ('94), vom Rath ('92), and others. Calkins ('97) figured tetrads in *Pteris* and *Adiantum* and interpreted them as a transverse and a longitudinal division. In the same year Osterhout ('97) figured the same in *Equisetum*. Belajeff ('98) and Atkinson ('99) figured a longitudinal and a transverse division in plant cells. Though different observers found minor variations in the details of tetrad formation, all agreed on the essentials; namely, that there was a longitudinal division of the chromatin thread followed shortly by a transverse division, thereby forming a number of segments equal to one half the number of somatic chromosomes. These segments were looked upon as each composed of two somatic chromosomes united end to end. In the ensuing divisions these segments were divided once longitudinally and once transversely, thus giving a qualitative reduction in accordance with Weismann's hypothesis.

On the other hand, the researches of Carnoy ('86), Boveri ('87), Hertwig ('90), and especially Brauer ('93) on *Ascaris* led them to conclude that both divisions in tedrad formation were longitudinal; that is, the tetrads arose by a double longitudinal division instead of by a longitudinal and a transverse division. The conditions in *Ascaris*, however, are complicated from the fact that the number of chromosomes in the somatic cells is very much larger than in the germ cells; therefore, it may be questioned whether the chromatin body dealt with in the germ cells is a true

chromosome in the sense in which that term is used for other organisms. Most of the investigators of this period, however, believed that, as a general thing, tetrads, in the strict sense, are not formed. Miss Sargant ('95) concluded that both divisions were longitudinal in *Lilium*. This was soon concurred in by Strasburger ('95), Farmer and Moore ('95) Dixon ('96), and by a number of other workers. Two years later Strasburger and Mottier ('97) figured a longitudinal and a transverse division in *Lilium* and several other angiosperms. Practically similar results were obtained by Ishikawa ('97) in *Allium*, and by Belajeff ('98) in *Iris*. Schaffner ('97), also working with *Lilium*, figured a transverse division in the first mitosis and a longitudinal in the second. Atkinson ('99) in *Arisaema* represents a tedrad formation which he interprets as a transverse and a longitudinal division, the transverse appearing in the first mitosis. In the same article he represents a transverse division in the second mitosis in *Trillium*. Atkinson attempts to reconcile the discordant views of the different investigators by the interesting explanation that in some plants there is a true reduction, while in others both mitoses are quantitative, and he even believes that "in the same plant qualitative reduction may take place in some cells, while quantitative or numerical reduction only takes place in others." Strasburger and Mottier soon changed their opinion and again believed both divisions to be longitudinal. The latter view was held by Gregoire ('99), McGregor ('99), Guignard ('99), Lloyd ('02), and others. Such, briefly, was the state of the question at the beginning of the present century. About the only conclusion one can draw from a review of the literature of the period is that a large majority of the investigators believed that both divisions are longitudinal and that, therefore, there is no true reduction.

Moore ('95) in his work on elasmobranchs found a unilateral massing of the chromatin at one side of the mother-cell nucleus previous to the formation of the chromosomes of the first mitosis and named this stage synapsis. Moore probably did not at the time appreciate the significance of synapsis nor know that he had so well named this which seems destined to prove the most important stage in the ontogeny of an organism. Little attention was paid to this work, as for some time synapsis was thought to

be an artifact. Moore firmly believed, however, that this unilateral massing of the chromatin was natural and said that "whatever the synapsis may eventually turn out to be it is evidently a cellular metamorphosis of profoundly fundamental character." He, as well as many later investigators, found that in many cases the chromosomes emerged from synapsis in the reduced number and frequently longitudinally split.

From the fact that synapsis was by many considered due to faulty fixation little attention was paid to it, and as a result some of the most important periods in the reduction stages have been overlooked. McClung ('02) holds that a unilateral massing of the chromatin — synapsis — is an artifact and says that he has not found it "when the material was well fixed and prepared. It has, moreover, been found possible to produce the appearance at will." He does not tell, however, how it may be produced at will. Schaffner ('06) seems to take somewhat the same stand, that synapsis is due to killing agents, though he finds it "usually present" in his own material just as the spireme is fully formed. While synapsis is still regarded as an artifact by some (Schreiner & Schreiner,'04) it is now very generally regarded as a constant and essential stage in reduction, so much so that one of the recent text-books, Coulter and Chamberlain ('03), considers it a constant morphological character of the mother-cell. That it is a real and not an artificial character I think there can be little doubt. In not one of the dozen or more forms examined in the present work was a unilateral contraction of the chromatin wanting at the proper stage. It was found to occur as often in megaspore as in microspore mother-cell. Though a number of different killing agents were used there was no variation in the effect produced. In such forms examined as *Salomonia*, *Botrychium*, *Dramia*, *Unifolium*, *Pedicularis*, and others where the sporangia are developed acropetally by a whole raceme or spike, all cells are under like conditions and a comparative study is not difficult. In the above-mentioned forms synapsis was always found at a certain stage in the development and persisted for some little time. Davis ('99) made a careful study of the developing sporogenous tissue of *Anthoceros* — a form peculiarly well suited for such a work — to determine whether the unilateral contraction of chromatin is due to killing

agents. He tested the effects of a number of different killing agents and found synapsis always to occur at the same period, and at no other, in the development of the mother-cell. Moore ('95) found it in cells which had simply been preserved in glycerine. But most convincing of all is the fact that Miss Sargant ('97) found synapsis in fresh material of *Lilium*.

Most of the recent papers on reduction, recognizing synapsis as a constant character of the mother-cell, have dealt with the question from a somewhat different standpoint, and, naturally, stages in the contraction of the chromatin, which formerly were discarded as artifacts, have been given careful study.

Farmer and Moore ('05), after a study of a number of plants and animals, offer a partial explanation of the synapsis stage which Moore had named ten years previously. According to their accounts a single spireme thread is organized which finally becomes contracted at one side of the nucleus in the vicinity of the nucleolus. This contraction stage persists for some time. Finally, the threads disentangle to some extent and form loops with one end of the loop at the nuclear membrane ("attached rather securely to the nuclear wall") and the other end in the vicinity of the nucleolus where there is still figured a considerable mass of contracted threads. Meanwhile as the threads have disentangled from the knot, first the chromomeres and later the remainder of the thread splits longitudinally. This longitudinal split soon closes up, however, so that in the ensuing stages there is little, if any, evidence of it; a shortening and thickening of the threads follows so that the sides of the loops are pulled into a somewhat parallel position. The number of these loops is found to correspond to the gametophyte (reduced) number of the chromosomes. The original thread is looked upon as composed of sporophytic chromosomes united serially and each of the loops is composed of two of these. There is now a separation of the loops to form V-shaped bivalent chromosomes. The apex of the V represents the part of the loop which was attached to the nuclear wall and is the point of union, end to end, of two sporophytic chromosomes. The arms of the V represent the portions of the thread which splits longitudinally and closes up again after the "first contraction" stage. This split sometimes

shows in the late prophases of first mitosis. Farmer and Moore find that the first mitosis is heterotypic and separates the arms of the V by a transverse division through the apex, thus separating whole sporophytic chromosomes. In the second mitosis the division is longitudinal and separates the parts of the thread formed by the longitudinal split of the earlier stages. Thus there is a true reduction. Farmer and Moore believe that in certain organisms the second division may be the heterotypic division, which of course would make no essential difference in the end results.

Essentially similar results to those of Farmer and Moore were found by Schaffner ('97) in *Lilium*, though he does not figure any synapsis (unilateral contraction of the chromatin). In a recent paper Schaffner ('06) in *Lilium* confirms his former results and states that synapsis is an artifact. So far as I am aware he is the only plant cytologist of the present time holding such a view of synapsis.

Mottier ('05) upon a reexamination of the microspore mother-cell of *Podophyllum* concludes again that the first division is a transverse or reducing division.

Strasburger ('04) gives a peculiar account of synapsis in *Galtonia candicans*. He finds that the sporophytic chromosomes lose their identity during the growth-periods and, in the early mother-cell, the chromatin collects in six centers (*Gamozentren*). Probably both paternal and maternal chromatin enter these centers which finally elongate to form a spireme. The spireme forms into six segments, each of which is composed of two chromosomes united end to end, and since there are six chromosomes in the gametophyte of *Galtonia*, these represent the bivalent chromosomes of the heterotypic mitosis. Thus there is a reduction in the first mitosis essentially in agreement with the results of Farmer and Moore ('05) and Schaffner ('06).

Montgomery ('00 and '01*a*) in work on *Hemiptera*, and on *Peripatus*, a form allied to the myriopods, finds that reduction occurs by an end to end fusion of somatic chromosomes in the late telophase in the last spermatogonial and oögonial division, that is, with the formation of the mother-cell nucleus. He considers this the synapsis stage even though it occurs some time previous to the unilateral massing of the chromatin which he

finds constant. Montgomery explains this union of whole chromosomes as a pairing of maternal with paternal chromosomes. These bivalents enter the contraction stage, become longitudinally split, and in the first mitosis are divided transversely, thus separating whole somatic chromosomes, while in the second mitosis the division is longitudinal, an equation division. Montgomery ('03, '05) confirmed these observations in later papers.

Sutton ('02) reports an end to end fusion in *Brachystola*, an orthopteran, in the late telophase in the last spermatogonial mitosis, but finds that the separation of these chromosomes does not take place until the second division following their union; thus the first mitosis is equational, the second reductional.

Dublin ('05*a*) in *Pedicellina*, a bryozoan, describes an end to end fusion at the end of spermatogonial and oögonial divisions and a separation of these, reduction, in the first mitosis. The second mitosis is equational. Haecker ('04) reported results essentially similar to those of Dublin ('05*a*) and Montgomery ('01).

Gregory ('04) in several *Pteridophyta* reports a formation of bivalent V-shaped chromosomes in the reduced number. These segment transversely with the first division and longitudinally in the second division, thus in essential agreement with Schaffner ('97) and Farmer and Moore ('05). Moore in later paper (Moore and Walker, '06) reports results in agreement with his earlier work.

Another group of recent investigators — Allen, Berghs, Gregoire, Miyake, Overton, Rosenberg, Schoenfeld, Schreiner and Schreiner, Miss Stevens, Winiwarter — obtain results somewhat at variance with those previously mentioned. Allen ('04), in a preliminary note on the microspore formation in *Lilium*, finds that after the formation of the mother-cell there is a long growth period in which the chromatin is in a reticulate condition. During the latter part of the growth period the chromatin changes from irregular reticulate masses into threads which become arranged in pairs, the moieties of each pair parallel, as they pass into synapsis. In synapsis the chromatin is massed in a tight knot at one side of the nucleus, often pressed against the nuclear wall with the nucleolus. As these parallel threads enter synapsis they move closer together and finally fuse to form a single thread which shows no evidence of its bivalent character for some time

after its formation. Just previous to the union of the two parallel threads their substance is differentiated into linin and chromatin, the latter aggregated into small granules, chromomeres. With the fusion of the threads the chromomeres fuse in pairs. The chromatin is in synapsis for several days. The threads emerge from synapsis and become distributed throughout the nucleus forming twelve loops, not unlike those figured by Farmer and Moore ('05), which segment transversely at or near the point where they are in contact with the nuclear wall to form the reduced number of chromosomes. Previous to this transverse segmentation there is a longitudinal fission of the thread, the chromomeres, which are still apparent, first dividing. Allen believes that this longitudinal fission represents a separation of the paired threads which fused in the presynaptic stages. He finds a second contraction stage when the chromatin threads are drawn away from the nuclear wall. This contraction, however, is not nearly so marked as in the case of synapsis. The first mitosis is longitudinal and probably separates the two threads which fused in synapsis, thus giving a true reduction. The heterotypic chromosomes are not, as a general thing, V-shaped, but rod-shaped as they pass to the poles, though often remaining attached at their equatorial end, thus forming a V-shaped body. The second division is also longitudinal and divides the daughter-chromosomes of the first mitosis.

Winiwarter ('00), suggested a view similar to Allen's as one of three ways in which reduction might be accomplished, and is strongly of the opinion that it is the most plausible explanation of reduction, as it explains the synaptic knot, which he believes to be a constant and important morphological character of the mother-cell.

Almost simultaneously with Allen's work appeared that of Berghs ('04*a*, '04*b*) in *Convallaria* and *Allium*, and of Schreiner and Schreiner ('04). They get essentially the same results as Allen, though Berghs believes there is not a complete fusion of the parallel threads in synapsis. Gregoire ('04), in whose laboratory Berghs worked, vouches for the accuracy of the latter's observations and strongly opposes the idea of an end to end fusion or a reduction by a transverse division. Berghs ('05*b*) in a later work on *Drosera*, *Narthecium*, and *Helleborus* confirms his former results.

Rosenberg ('03, '04*a*, '04*b*) in *Drosera* obtains especially interesting results from a hybrid of *Drosera longifolia* with *D. rotundifolia*. The gametophyte of *D. longifolia* has twenty small chromosomes, while the gametophyte of *D. rotundifolia* has ten large ones. Therefore in the hybrid sporophyte there are thirty, while in the gametophyte there are not fifteen but twenty chromosomes. Rosenberg finds that, in the early prophases of the first mother-cell mitosis of the hybrid, there are twenty chromosomes, ten of which are bivalent, while the other ten are univalent. These ten bivalents are each composed of a larger and a smaller part. Rosenberg believes that the ten large chromosomes from *D. rotundifolia* fused with ten of the smaller ones of *D. longifolia*, thus leaving the other ten small chromosomes univalent. The first mitosis separates by a longitudinal fission whole chromosomes. This is true for others than the hybrid. Thus there is a true reduction in the same sense as in the results of Berghs ('04*a*, '04*b*, '05*a*) and of Allen ('05*a*). The second division is also longitudinal.

Miyake ('05), in a number of monocotyledons, states that the threads are not fully formed previous to synapsis but that masses of chromatin — not chromosomes — fuse and later organize parallel threads which separate with the first mitosis. He finds the second mitosis homotypic.

Overton ('05), in a number of dicotyledons, gets essentially identical results with those of Allen, though he figures masses of chromatin — "protochromosomes" — which he considers the equivalent of the sporophytic chromosomes. These masses pair — but do not fuse — during synapsis and separate longitudinally in the first division. Allen ('05*b*) in a later paper confirms his previous results ('05*a*). Miss Stevens ('05), in *Aphis*, finds that reduction in the spermatocytes is effected by a longitudinal pairing of the chromosomes.

Schreiner and Schreiner ('06) in a recent paper on *Tomopteris*, an annelid, report results essentially similar to those found in the present work. In a number of excellent figures the slender chromatin threads are shown to arrange themselves parallel and, commencing at one pole of the nucleus, conjugate longitudinally. The threads then become shorter and thicker as the first division is approached. After the parallel threads have conjugated the

moieties often remain separated for a short distance at their ends and by this means these investigators believe they can follow the history of the thread through the prophases of the heterotypic division. The chromosomes of the prophase assume ring- and cross-forms similar to many of the others recently figured for animals and give appearances that would indicate that the first division is transverse. Schreiner and Schreiner, however, are confident that both divisions are longitudinal, the heterotypic taking place along the line of original fusion of the prereduction chromosomes.

Thus there are, evidently, two schools of the more recent investigators which seem to differ radically in regard to the details of reduction, though they are in agreement on one essential point; namely, that the first division is heterotypic and separates whole somatic chromosomes which had retained their individuality through the growth period of the organism.

The present work was taken up with the hope of throwing some light upon the phenomenon of synapsis and its relation to reduction division. A number of forms have been examined. The results of observations upon four of the forms are presented here. Results from other forms will follow in a succeeding paper. Observations were made upon sporogenous tissue in all stages from early archesporium to spore formation, but chief attention was given to synaptic and presynaptic stages.

The forms chosen represent four groups: namely, pteridophytes, gymnosperms, monocotyledons, and dicotyledons. As the results agree in the essential points, they seem to indicate that the reduction process is the same throughout the plant kingdom.

No pretense is made of citing all the literature on reduction, nor of going into a detailed discussion of the philosophical aspects of the question. Both of these points have been admirably taken up recently by Allen ('05*a*), Davis ('05), Gregoire ('05), and several others.

The material for this work was collected in the vicinity of New York City in the spring of 1905, except in the case of *Botrychium*, which was collected in Indiana and Ohio the year previous. The ordinary methods of microtechnique were used in making the preparations for study. Many preparations were made of each type examined.

ACER PLATANOIDES L.

This plant presented especially good material for study. The chromosomes are few and there is an exceedingly large amount of sporogenous tissue in one small flower cluster. The form has the disadvantage, however, of having exceedingly small sporogenous cells, as will be noted from the drawings. Only microsporangia were examined, though both micro- and megasporogenous tissue were examined in a few cases in *A. Pseudo-Platanus*, which apparently did not differ essentially from *A. platanoides*.

The winter is passed with the sporogenous tissue in the early mother-cell stage. In this stage (figure 1) the cytoplasm is exceedingly dense and granular with a very few small vacuoles, and it takes stain strongly. There is as yet no rounding-off of the cell-wall and no intercellular space in the sporangium. The cells are all characterized by a relatively large nucleolus which appears to contain small vacuoles (figure 1). The chromatin is small in amount and is collected in small granules at the periphery of the nucleus, sometimes, apparently, even pressed against the nuclear membrane. Owing to this position of the chromatin the number of these granules could not be determined. Figure 1 shows only a sectional view of the nucleus. Connecting the chromatin granules are exceedingly fine linin threads which will also occasionally be found running across the nuclear cavity; in the latter case they are usually in contact with the nucleolus. Occasionally at the point of contact of linin thread and nucleolus the latter will be found bulged out forming a small papilla. It was impossible to determine definitely the significance of this, though it suggested at once the formation of the true chromatin thread from the material of the nucleolus. In some preparations this nucleolar papilla looked much like one of the small vacuoles escaping. Later, however, in examining the same phenomenon in *Claytonia virginica* there seemed to be very strong evidence that there is a flowing of material from the nucleolus to the linin-chromatin threads. At this stage it is impossible to determine any definite arrangement of the threads with reference to each other.

As development continues, the threads leave the periphery and traverse the nuclear cavity in all directions (figure 2). The chromatin constantly increases in bulk, chiefly, it appears, by an in-

crease in size of the chromatin granules, and also by spreading along the thread. As chromatin increases along the linin thread it is generally impossible to distinguish definitely between linin and chromatin, and the appearance of this and much of the other material used recalls the theory that linin and chromatin are merely different phases of the same substance. Figure 3 shows a still greater increase in chromatin and at several places an approximation of threads in pairs as at *a* and *b*. An indication of the same pairing can be seen also at *a* in figure 2. By the time the stage shown in figure 4 is reached the cell has increased greatly in size and shows a decided rounding-off of the wall. The nucleus shows, proportionately, a greater increase than the cell. The nucleolus, however, does not partake of this increase in growth, or at least to a very limited extent. The cytoplasm has become more reticulated in structure; the chromatin has become more evenly distributed over the thread and there is an evident pairing of threads, which, however, is more marked in a slightly later stage (figure 5). In this figure no less than eight distinct pairs of threads or portions of threads can be made out. Most of these pairs seem to be in contact with the nucleolus or very near to it. In stages but little later the pairing of threads is still more evident, as shown in figures 6–12. Figures 7–11 are taken from five adjoining cells. Figures 6–12 show chromomeres actually in contact in many instances, while the portion of the thread between the chromomeres seems to have changed but little from its condition in much earlier cells where it takes the stain very lightly. Chromomeres in many instances show an actual flowing together, as shown in figure 12, which is slightly enlarged. That this is a pairing and not a split seems certain to one examining the preparations. It is not difficult to be sure of the stage in the development of the mother-cell in *Acer*, owing to the gradual change that takes place in the cytoplasm, which shows a reticulated nature as the cell gets older, and owing to the gradual increase in the size of the nucleus until near the synapsis stage, and because, also, of the changes that take place in the cell-wall, etc. A gradual approximation of the threads in pairs can be followed until the chromomeres actually begin to blend in stages shown by figure 13, a stage just previous to the close synaptic knot. This appearance of the threads is undoubtedly what the earlier investi-

gators on reduction called the first longitudinal split. Figure 12 is a portion of a thread from a stage a little earlier than that shown in figure 13. It shows the chromomeres blended while the linin portion of the thread is not in contact. In looking at a preparation like this it is difficult to think of it as a split, especially if one considers the chromatin as the active element of the nucleus. The slender threads are relatively widely separated in the presynaptic stages and as they approach the knot stage they come closer together until in the knot condition they are so closely blended that only occasionally, figures 14 and 15, can two threads be seen. These are evidently the same stages figured by Allen in *Lilium*, Berghs in *Convallaria*, *Allium*, etc.

That the synaptic knot is a region of great activity is indicated by the way in which it resists the extraction of stains (safranin and iron-haematoxylin). That this is due not to the mass effect alone is shown by the fact that a small section cut from one side of the knot behaves in the same way. The contraction of the chromatin threads into the synaptic knot invariably occurs at one side of the nuclear cavity and in close contact with the nucleolus, the latter being almost surrounded by the threads at times. Often loops of thread or threads extend outward some distance from the knot, but these loops are always few in number — much less than the number of chromosomes — and show no such regularity in arrangement and number as those figured by Farmer and Moore ('05). Montgomery ('05) reports that he finds the synaptic knot always on the side of the nucleus bordering upon the greater bulk of cytoplasm in the cell. This does not accord with my observations. In fact the knot seems to be as often, if not more often, on the side of the cell where there is the least cytolasm. It was generally found, however, that in any one sporangium or group of sporangia all the knots occupy the same relative position in the nuclei. I offer as a tentative explanation of this that the chromatin mass is of greater density than the nuclear sap and the position of the nucleolus and knot is due to gravity. From the material with which I worked it was impossible, however, to determine this for a certainty.

As the threads emerge from the synaptic knot they show no differentiation into linin and chromatin, but instead a continuous

chromatic character, and are much thicker than when entering the knot. Whether this obscuring of the so-called linin by the chromatin is due to the linin taking on chromatic properties — becoming chromatin — or whether the chromomeres have increased until they have obscured the linin is impossible to say though the former appears to be the more probable. The thread is not even in outline but is thickened at short intervals indicating probably the original chromatin centers or chromomeres. From the position of the nucleolus with reference to the knot it would seem that it must play some part in synapsis, yet it seems to have suffered no change either in size or capacity to take stain as a result of synapsis. However, if the above explanation in regard to the position of the knot is correct, the close proximity of the chromatin and nucleolus may be merely incidental.

As soon as the threads commence to disentangle from the knot, evidence of a longitudinal fission can often be seen (figures 16–20). Whether this splitting is a separation of the threads which paired in the presynaptic stages cannot be determined for a certainty, although it seems very probable, as many close synaptic knots will have portions of threads on their periphery which always show a paired character. Work of Montgomery ('00, '01*a*, '05), Sutton ('02), McClung ('02), Rosenberg ('04*a*) would seem to indicate beyond a doubt that the reducing division occurs along the line of original fusion. Wilson ('05*a*, '05*b*, '06) in his work on *Hemiptera* showed with special clearness that certain univalent chromosomes —the "idiochromosomes" and the "m-chromosomes" — unite in synapsis and the reduction division separates these univalents with their individuality unimpaired. Since this pairing and subsequent separation of the moieties has been so clearly proved for certain chromosomes it may not be unreasonable to expect it to occur between all chromosomes. In other words, in *Acer* there is not a complete fusion of threads in synapsis, but the individual threads probably retain their identity through the synaptic stages.

From synapsis on to the final formation of the heterotypic chromosomes it is easy to follow this longitudinal fission. The threads continue to increase in thickness (figures 19 and 20), but the moieties remain in close contact with each other for some time.

Finally there is a decided shortening (figure 20) of the threads and the paired portions show more of a tendency to separate. It is about this stage that we have the first evidence of a transverse segmentation of the threads into chromosomes. As the chromosomes pass through the prophase of the first, or heterotypic, division they are always bivalent in character and at first the parts of each bivalent are often twisted several times upon each other and they are either in contact with the nuclear membrane or close to it. During the prophase the parts of the bivalents untwist so as to give rings, 8's, Y's, V's, X's, and the various other forms so characteristic of this stage (figures 21–32). It is easy to see how these forms have been so often interpreted as tetrads formed by a longitudinal and a transverse division. There is here, however, not the slightest evidence of a transverse divison of the heterotypic chromosomes; on the other hand, the evidence seems strong that there is simply a separation of univalent parts of a bivalent chromosome which attained its bivalent character in synapsis. From the time they are formed the chromosomes gradually become shorter and thicker until metaphase is reached when they are almost spherical in shape. After synapsis is reached the nucleus ceases to increase in size. The cytoplasm immediately surrounding the nucleus becomes much more dense and shows a decided fibrillar character (figure 15), probably the beginning of the spindle-fibers. As metaphase of the first division of the mother-cell is reached the chromosomes are closely crowded together and the spindle is very small though very clearly defined (figure 35). Repeated counts of the chromosomes both in this and the entire prophases (figures 33 and 34) indicate that the number is probably eleven. Individual differences in the size and shape of the chromosomes were evident in nearly all nuclei. Some were three times the size of others (figures 33 and 34). Certain chromosomes by their shape and size could almost always be identified in the different nuclei. It will require further work to determine what may be the significance of these size differences, but that they are constant there seems little doubt.

From metaphase of the heterotypic division to the final spore formation the stages are passed through very rapidly. There seems no doubt that the second division is homotypic in character.

SALOMONIA BIFLORA (Walt.) Britton

This form affords especially good material for study. The acropetal development of the flowers in the inflorescence, which at the time of reduction is still quite short, enables one to get in each section a series of stages in the development of sporogenous tissue.

In the very early mother-cell the cytoplasm is in a very fine alveolar or granular condition. There are generally present several nucleoli (figure 36). As the cells get older the threads of the reticulum become coarser and take the stain more strongly; the cytoplasm losing its alveolar character, later becoming fibrillar and containing many conspicuous deeply staining granules (figure 44).

The stages are passed through quite rapidly, so that material must be collected at frequent intervals in order to be sure of stages, though the cell seems to pass some time in the stage shown in figure 36. In order to meet this condition, in part, many rhizomes of the plant were taken up early in the spring, brought into a greenhouse and forced. Collections were made from these at all times of day. Material was also fixed in the field at different times.

As soon as the mother-cell commences to increase in size the chromatin commences to increase and is organized into threads which, as in *Acer*, leave the nuclear wall and traverse its cavity. The chromomeres increase in size and seem to spread along the linin thread, which either becomes chromatin or is obscured by it until at the contraction stage of synapsis no trace of linin, as such, is in evidence. With the change in the chromatin from a reticulum to a spireme there begins an arrangement of threads parallel to each other which show as far back as the stages shown in figures 37 and 38. This parallelism becomes more marked — even more than in *Acer* — as the contraction-stage is approached (figures 39–44). Here, too, the collection of the threads near the nucleolus or the movement of the two to the same side of the nucleus is apparent.

As the chromomeres approach each other they seem to become much more active, increasing in size and staining more strongly, than when at a greater distance even in the same nucleus. This is shown in figure 43*a*, where the threads are still widely separated. A careful examination of the material from which figures

39–44 were made convinces me that these parallel threads are in process of conjugation and not in process of fission as undoubtedly most investigators formerly and many at the present time have interpreted their parallel arrangement. Compare, for instance, figures 39 and 40 with figures 43 and 44. There can be no question in regard to the age of the two, judging merely from the extra-nuclear structures, as the character of the cytoplasm, the rounding-off of the cell-walls, and also the degree of development of the other organs of their respective flowers. Then there is the great difference in size in the nuclei themselves, as shown by the figures, which were made by careful camera drawings. While there is some slight variation in size of the nuclei in the various plants there is a very evident gradual increase in size from the time the mother-cell is formed up to synapsis. In the earlier stages (figures 39 and 40) the chromatin is for the most part near the nuclear wall and it is difficult to represent it all in a drawing, therefore these two figures are sectional views of the nuclei. At these stages the parts of a pair are much farther from each other than in the later stages (figures 43 and 44). In stages shown by figures 43 and 44 the threads have for the most part left the nuclear wall and are becoming massed in the nuclear cavity. They are very close together, in many places actually in close contact so as to appear but one thread, while in other places only the chromomeres are in contact. Where the threads are actually in contact no differentiation of the thread into linin and chromatin is possible; the whole thread appearing to be composed of a continuous mass of chromatin as in the threads in the postsynaptic stages. The bivalent character of the threads disappears entirely in synapsis (figure 45) except at times where a portion of a thread can be seen on the side of a synaptic knot, when this bivalent character can be made out.

Often synaptic knots like the one in figure 46 can be found with portions of threads projecting from the chromatin mass. These invariably show a bivalent character. Figure 46 is probably of a nucleus just coming out of synapsis. Later stages of the thread, disentangling from the knot (figures 47 and 48), show clearly the bivalent character. The univalent parts of these bivalents undoubtedly represent the threads seen in presynaptic stages.

Later there is a transverse segmentation (figure 48*a*) to form the chromosomes of the immediate prophase. Several of these still show their bivalent character though not to such a marked extent as in the case of *Acer* (figure 49).

What may be the significance of the small spherical bodies in the nucleus at this stage (figure 49*a*) was not definitely determined, though it seems probable that they are a disorganized nucleolus, as there appears to be no regularity in their number. The number of the chromosomes is probably seven or eight though not enough counts were made in this case to determine definitely. That there are individual differences as to size, shape, etc., which are constant in the different cells, seems evident. As the chromosomes are arranged in the plate at metaphase they have the short, thick appearance of the usual heterotypic chromosomes (figures 50 and 51). But few of them show a bivalent character and it is impossible to tell whether they are divided along the line of their original conjugation or not.

One point of interest in the metaphase of the heterotypic division is that in a very large number of the cells one of the chromosomes appears to pass undivided to one pole considerably sooner than the others (figures 50 and 51), seeming, generally, to reach the pole about the time that the split is complete in the other chromosomes (figure 51). When first noticed it was thought the position of this chromosome was due to faulty sectioning. Upon closer examination, however, it was seen that this was not the case, but that the behavior of this chromosome is undoubtedly different from that of the others. What the significance of this is I hope to find by later work. The fact undoubtedly suggests a comparison of this chromosome with the "accessory" or heterotropic chromosome found in the spermatogenesis of *Orthoptera*, *Hemiptera*, and other insects, but in view of Wilson's ('05*a*, '05*b*, '06) results regarding the relation of this chromosome to sex production it seems improbable that it should occur in an organism which is essentially hermaphrodite. No chromosomes exactly similar to this were noted in the other forms studied, though in many of them could be found a chromosome that divided earlier than the others. These may possibly correspond to the idiochromosomes of Wilson but there is no direct evidence of this. If the heterotropic chromo-

some passes undivided to one pole of the nucleus in the first division and divides in the homotypic division, one half of the microspores should contain each one more chromosome than the other half, but I have no direct evidence to show that such is the case. Wilson in his recent investigations upon chromosomes seems to have proved beyond a doubt that these chromosomes of unusual behavior are in some way connected with sex-determination.

He finds in a number of *Hemiptera* that the oögonial cells contain one more chromosome than the spermatogonial cells, the latter having an odd number and the extra chromosome (heterotropic) goes over undivided in the first maturation division. Thus half of the sperms have the same number of chromosomes as the unfertilized eggs, while the other half have one less than this number.

In the spermatogonia of other forms he finds that in one of the bivalent chromosomes the univalent parts are of unequal size. As a result it divides unequally and one half the sperms have one chromosome (idiochromosome) smaller than the other half. In the oögonial division of this group all chromosomes divide equally.

In one form (*Nezara*) Wilson finds that all the heterotypic chromosomes divide equally in both sexes. One pair of chromosomes, however, agrees in behavior with the idiochromosomes of the previous group though they have not yet become differentiated in size. Wilson's work gives the most tangible evidence yet obtained upon the behavior of the individual chromosomes in the germ cells and should the idiochromosomes or their homologues prove to be of general occurrence a most important advance will have been made in this field of cytology.

Even if the heterotropic chromosome of *Salomonia* is of the same significance as in the *Hemiptera* studied by Wilson, its behavior and later history will not be so simple on account of the fact that *Salomonia* is a bisporangiate plant. It may, however, be related to prepotency of microspores.

GINKGO BILOBA L.

While the microsporangia of *Ginkgo* are very abundant and accessible and preparations from them are made with little diffi-

culty, it did not prove as profitable a form for study as some of the others which were used.

The nuclei contain a great abundance of chromatin which in the very early mother-cell is in a coarsely reticulate condition. In this stage, however, can be seen evidence of both chromomeres and linin, often in a thread-like arrangement (figure 52). No regularity in the arrangement of these thread-like masses of chromatin can be discerned except that they appear more abundant near the periphery of the nucleus. There are present several nucleoli which are generally surrounded by a clear area free from chromatin. This condition I have found to obtain in the early mother-cells of a number of other forms. There seems to be no attraction or connection between chromatin and nucleolus as is found so often in later stages. In fact this behavior of the chromatin toward the nucleolus and also the common arrangement of chromatin at the periphery of the nucleolus indicates that, at this stage, there may be a mutually repellant force existing between the chromatin units, or perhaps groups of units. Nor is there anything unreasonable in this idea, if, as is believed by many cytologists, the maternal and paternal chromatin remain separate during the presynaptic period of the first generation.

The relative amount of cytoplasm in the microspore mother-cells is exceedingly small as compared with any other form examined (figure 53).

As the development proceeds the chromatin leaves the nuclear wall and definite spireme threads are formed. Very shortly following this, the threads can be seen arranged in pairs (figure 53), and show a differentiation into linin and chromatin. At this stage the moieties are very seldom in contact. The threads do not appear to be continuous in these early stages though they do later. They change gradually from ragged, irregular, discontinuous threads to those of a more continuous, even outline and are of a deeper staining capacity. In these threads the chromomeres show quite clearly. Owing to the difficulty of showing all of the chromatin of a nucleus at this stage only sections of nuclei are figured (figures 53 and 54). In these later stages there is seldom more than a single nucleolus, which is, however, always much larger than any one of the nucleoli found in the earlier stages.

Whether the one large nucleolus resulted from the union of several smaller ones could not be ascertained, though this seems probable. Around this nucleolus the chromatin threads show a marked tendency to collect. It was also noted, in other forms as well as *Ginkgo*, that the moieties are in contact, or at least closer together, in the vicinity of the nucleolus (figure 54). The contraction of the chromatin continues until a dense knot is formed at one side of the nucleus (figures 55 and 58). In stages just previous to the close knot (figure 55) and in those following, there is very rarely present a nucleolus in *Ginkgo*. This is a marked difference from the nucleolar behavior in other forms and indicates that the nucleolus may be playing a more prominent part in chromatin formation than generally supposed. This unusual behavior of the nucleolus may be correlated in some way with the other unusual cytological conditions in *Ginkgo*.

As the chromatin threads extend from the synaptic knot they nearly always show their paired character, especially if the closely contracted stage is not yet reached, as in figure 55. In these portions of the threads that are still free from the knot the chromomeres are clearly discernible (figure 55), while after they have been drawn closely into the knot the threads appear as a continuous chromatin-mass (figures 56 and 57).

As the threads emerge from synapsis they are much shorter, thicker and more homogeneous throughout than in the presynaptic stages (figure 59).

Their bivalent character can be made out with difficulty until the chromosomes are finally formed in prophase when it is quite evident (figure 60). The twelve chromosomes figured here are from a camera drawing of an unusually good early metaphase view. While this number may not prove correct, it corresponds with a number of other counts.

Owing to the fact that a blepharoplast is formed in the male gametes of *Ginkgo*, it was thought worth while to make a search for centrosomes in the reduction divisions where they would probably be in evidence if they exist at all. No structure of any kind which could be interpreted as a centrosome could be found, the spindles being very short and thick.

BOTRYCHIUM OBLIQUUM Muhl.*

From one standpoint *Botrychium* furnished one of the best forms that was studied. Owing to the peculiar development of the sporangium, an account of which was given in a previous paper (Cardiff, '05), it is possible to be very sure of the stages in development with which one is working. It has the disadvantage, however, of having a large amount of chromatin and many chromosomes.

The early archesporial nuclei contain each several nucleoli. The chromatin in the resting condition does not form a true reticulum, but is in the form of short, broken threads which seem to be composed of small chromomeres and very slender threads of linin. Figure 61 is from an archesporial cell some five or six divisions previous to mother-cell formation. The nuclei throughout the development of the archesporium are similar to this.

With the formation of the mother-cell, these chromatin threads increase in staining capacity. The chromomeres themselves increase in size, especially in the direction of the length of the thread, exactly as observed in many of the other forms studied. At the same time there is an evident pairing of threads or parts of threads (figure 62). When these paired threads can first be seen in the early mother-cell nuclei, they are very seldom in contact at any point. With the growth of the cell the moieties approach each other until in many places, especially in the vicinity of the nucleolus, the chromomeres come in contact (figure 63). The early stages of the mother-cell are passed through quite slowly, but as soon as the chromomeres of each pair commence to come in contact there is a rapid contraction of the threads in the vicinity of the nucleolus. At the same time the individual threads thicken considerably and are apparently continuous (figure 64). Here again the chromatin is so abundant that it is impossible to figure accurately an entire nucleus.

The shortening and thickening of the threads continues (figures 65–67) until they are finally all in synapsis (figure 68). The chromatin seems to remain in synapsis longer than in any of the

* This material is from the same plants from which previous studies were published. *Cf.* Botanical Gazette 39: 340. The plant there referred to as *Botrychium ternatum* is really the American ally, *B. obliquum* Muhl. The genuine *B. ternatum* is an Asiatic species not known in the United States.

other forms studied, though this may be due simply to the general slow development in *Botrychium*. Differing from the other forms described, the nucleus of *Botrychium* continues to increase in size for some time after synapsis.

As the threads come out of the contracted condition in synapsis they are short and thick and show a bivalent character (figure 69). They disentangle until they are uniformly distributed throughout the nucleus (figure 70), meanwhile continuing to shorten and thicken. Later they can be seen dividing transversely to form the chromosomes (figure 71). These contract until in the later prophase they are almost isodiametric (figures 72 and 73), yet practically all show a bivalent character. In fact, from synapsis to metaphase of the first division, the bivalent character of the threads and chromosomes is always evident. That the univalent parts of these bivalents represent the threads which conjugated in synapsis seems highly probable.

SUMMARY OF RESULTS

Synapsis is not an artifact, but a constant morphological character of the mother-cell.

The synaptic knot is always around or in contact with the nucleolus.

The unilateral position of the synaptic knot and nucleolus is probably due to gravity.

There is a gradual increase in size of the nucleus up to the time of synapsis.

There is an arrangement of chromatin into two or more threads previous to synapsis.

The presynaptic threads arrange themselves in pairs, longitudinally, and move together as synapsis is approached, finally fusing in synapsis.

In the fusing of the threads the chromomeres generally fuse in pairs.

Previous to synapsis the chromomeres are evident and connected by a slender thread of linin. After synapsis the thread is homogeneous throughout; that is, there is a marked difference in appearance of presynaptic and postsynaptic chromatin.

From the fact that in sections of close synaptic knots the threads still show their bivalent character, the identity of the individual threads probably is not lost in synapsis; *i. e.*, there is not a complete intermingling of chromatic substance in the bivalent thread.

The thread splits longitudinally in the first mitosis, probably along the line of previous fusion.

All of the chromosomes, at least in some species, do not behave alike in the reduction divisions.

Considerable difference is found in the size of different chromosomes in the same species.

Synapsis is probably the end-result of fertilization and a stage of great chemotactic activity.

CONCLUSION

From the foregoing results it will be seen that there is considerable uniformity in the behavior of the chromatin in the reduction phases of the forms studied. The results are largely in accord with those of Allen ('05) and Berghs ('04), though they differ to this extent, that there was observed no constant and definite stage that could be called a second contraction period, and there was rarely found any opening out of the moieties of the bivalent spireme after they had once joined. However, in *Acer* (figures 16–33), and several of the other forms which are not included in this paper, there is a slight separation of the moieties after the formation of the heterotypic chromosomes, which is partly due, no doubt, to the twisting of the chromosome as it is being pulled into the metaphase.

From the results obtained it seems highly probable that with the fusion of the gametes in fertilization there is a nuclear but not a chromatin fusion and that the maternal and paternal chromatin retain their identity throughout the sporophytic existence of the plant, finally fusing, in so far as it fuses at all, in synapsis. That is, the sporophyte is a sort of double-celled phase of the organism. Thus Cook and Swingle ('05), in an interesting article, argue that the sporophyte is not an asexual but a highly sexual generation or phase, in that it is produced "during the actual process of conjugation." These writers hold that "it was not the reduction to fewer chromosomes, but the retention of the double number, that constituted the important step in sexual reproduction and made

possible the evolution of complex higher organisms." If, as is generally admitted, the chromatin controls the metabolic activities of the cell, it would seem that the above theory is not without considerable foundation. The familiar fact, that an offspring more often possesses certain characters of the one parent to the exclusion of the other, would indicate that it is the chromatin of the latter that is controlling the physiological processes of the organism.

Nor are we without evidence that the maternal and paternal chromatin remains distinct during the sporophyte phase. Blackman ('98), Chamberlain ('99), and Miss Ferguson ('04) have shown, in *Pinus*, that the maternal and paternal chromatin do not fuse with the union of the gametes. Murrill ('00) observed the same behavior of the gametes in *Tsuga*, and similar results have been reported for a number of other gymnosperms and in *Onoclea* by Shaw ('98). Dublin ('05*b*) reported a similar phenomenon in *Pedicellina*, a bryozoan. But it is to the work of Moenkhaus ('04), of Herla ('93), of Haecker ('95*b*), of Ruckert ('95), and of Zoja ('95) we must turn for the best evidence on the independence of the paternal and maternal chromatin. Moenkhaus, in working with hybrid fishes, found that the maternal and paternal chromatin remained distinct until the third division in the embryo. He was able to follow this with especial clearness owing to the fact that the chromosomes of one parent, *Fundulus*, were much larger than those of the other parent, *Menidia*. Haecker and Ruckert in *Cyclops*, and Herla and Zoja in a hybrid *Ascaris* have also found that the chromatin of the two parents retains its identity through several divisions in the embryo. Since it is conclusively proven that the maternal and paternal chromatin retain their identity through several cell-generations, there is no reason why it should not be expected to do so through many generations, in fact, the latter seems highly probable.

If the above is true, the explanation of synapsis is that it is the end-result of fertilization. Thus the two phenomena of fertilization — stimulus to growth and mingling of ancestral characters — are quite widely separated, the former coming at once with the union of the gametes, and the latter with synapsis. The idea — not new — that the offspring is not the offspring of the parents, but of the grandparents, would find support in the results obtained.

In concluding it may be advisable to compare the results obtained with those reported from other recent work. Gregory ('04) reports a presynaptic longitudinal fission; similar results have been reported by others. One is tempted to ask, what can be the significance of this? Why should the chromatin threads split and then fuse again in a close synaptic knot? Whatever the behavior of the chromatin may prove to be, it is undoubtedly a purely physical process, and like many other natural phenomena that have been explained, will turn out to be a much more simple process than was previously expected.

Likewise the results of Farmer and Moore, Schaffner and others present many mechanical difficulties and — without in the least questioning the accuracy of the work done by these investigators — would indicate that we are still very far from a solution of the reduction problem. Thus one is obliged to think of the paternal and maternal chromosomes having arranged themselves alternately in a spireme previous to synapsis, a process presenting some difficulties. Then, if the union of paternal and maternal chromosomes takes place at the outer ends of the loops, that is, in those portions of the thread farthest from the knot, this is the synaptic point, and the knot in which the opposite ends of the loops are collected is not a true synapsis — that is, a fusing together of parental chromatin. In other words, the contraction stage is still unexplained. The same may be said of cases where an end-to-end fusion of chromosomes is reported as occurring in the telophase of the last spermatogonial and oögonial (or archesporial) division. It is quite conceivable that some of the chromosomes of unusual behavior reported in animals by Montgomery and Wilson might conjugate much earlier than the synaptic stage, as they have been shown to do much later, but if there is a general conjugation of the chromosomes with the inception of the mother-cell the contraction stage still remains unexplained. That a tightly coiled and contracted condition of the spireme is a condition conducive to splitting is highly improbable from a physical standpoint.

On the other hand, if the results obtained by Allen, Berghs, and those given in the present work prove to be the general condition the contraction stage is a true synapsis. It is a region, or

stage, of great chemotactic activity, which probably accounts for the way it retains dyes. It is the critical stage in the history of an organism. The heterotypic division immediately following it is, then, not a true mitosis, but, as Farmer and Moore have suggested, merely an intercalated phase in the ontogeny of an organism; a phase for the purpose of bringing about the distribution of the parental characters and causing the necessary variation in the progeny of an organism.

The bearing of this union of parental chromatin in the prereductional stages upon the principles of Mendel was first discussed by Wilson ('02), Cannon ('02 and '03), and Sutton ('03). The present work would indicate that the parental chromatins are brought into much closer relationship than was at first supposed by these workers. They are probably brought into such close relationship that there is a more or less blending or complex interchange of characters. DeVries ('03) suggests that in the case of an intimate blending of the chromatins there is possible an interchange of pangens which would, in many cases, approach Mendel's ratios. From the cytological work that has been done in the past six years it is evident that the explanation of Mendel's laws lies in the structure of the germ-cells. While much has been accomplished along this line, and we seem nearer a solution of the problem than ever before, it is equally evident that we are very far from a final explanation of heredity.

From the results of recent investigators it seems possible that there is not a strictly uniform behavior of the chromatin in synapsis, and that there may be considerable variation in the distribution of hereditary characters.

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Explanation of plates 12-15

All figures were made with Spencer 1.5 mm. objective and Leitz ocular, and camera lucida. The original drawings were reduced one half in reproduction. Except where otherwise indicated the magnification of the figures is × 2300.

ACER PLATANOIDES

FIGURE 1. Early mother-cell. Sectional view, only, of nucleus; chromatin at periphery of nucleus.

FIGURE 2. Mother-cell showing increase in chromatin and formation of threads. Parallel threads, *a*.

FIGURE 3. Later stage of mother-cell nucleus; threads parallel at *a* and *b*.

FIGURE 4. Nucleus of mother-cell.

FIGURE 5. Mother-cell; several pairs of parallel threads preparing for synapsis.

FIGURE 6. Presynaptic nucleus a little later than figure 5.

FIGURE 7. Paired chromatin threads from a presynaptic nucleus.

FIGURE 8. Paired presynaptic threads.

FIGURE 9. Paired presynaptic threads.

FIGURE 10. Paired presynaptic threads; moieties in one in close contact, apparently twisted upon each other.

FIGURE 11. Portion of presynaptic nucleus.

FIGURE 12. Pair of threads just previous to synapsis; chromomeres in contact and apparently fusing; linin portion of thread not yet in contact. Slightly greater magnification than other figures.

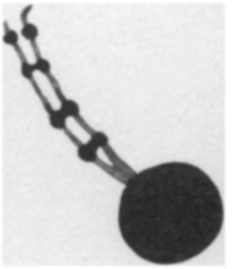

FIGURE 12*

FIGURE 13. Presynaptic mother-cell; threads contracting at one side of nucleus with nucleolus; moieties much closer together; cytoplasm becoming more dense in neighborhood of nucleus.

FIGURE 14. Contraction of chromatin threads just previous to close synaptic knot; parallel fusing of threads evident in looser portion of knot.

FIGURE 15. Synapsis; projecting end of thread showing bivalent character.

FIGURE 16. Chromatin threads just leaving synapsis; chromomeres no longer evident, but thread homogeneous throughout.

FIGURE 17. Portion of postsynaptic nucleus showing threads disentangling from synapsis.

FIGURE 18. Postsynaptic nucleus just after threads have left knot; bivalent character of threads.

FIGURE 19. Shortening and thickening of postsynaptic threads.

FIGURE 20. Stage a little later than figure 19, showing beginning of transverse division.

FIGURE 21. Bivalent chromosome just after transverse division.

FIGURES 22 and 23. Stages showing shortening and thickening of chromosomes.

FIGURES 24–32. Bivalent chromosomes of prophase of first division; various stages in shortening and thickening.

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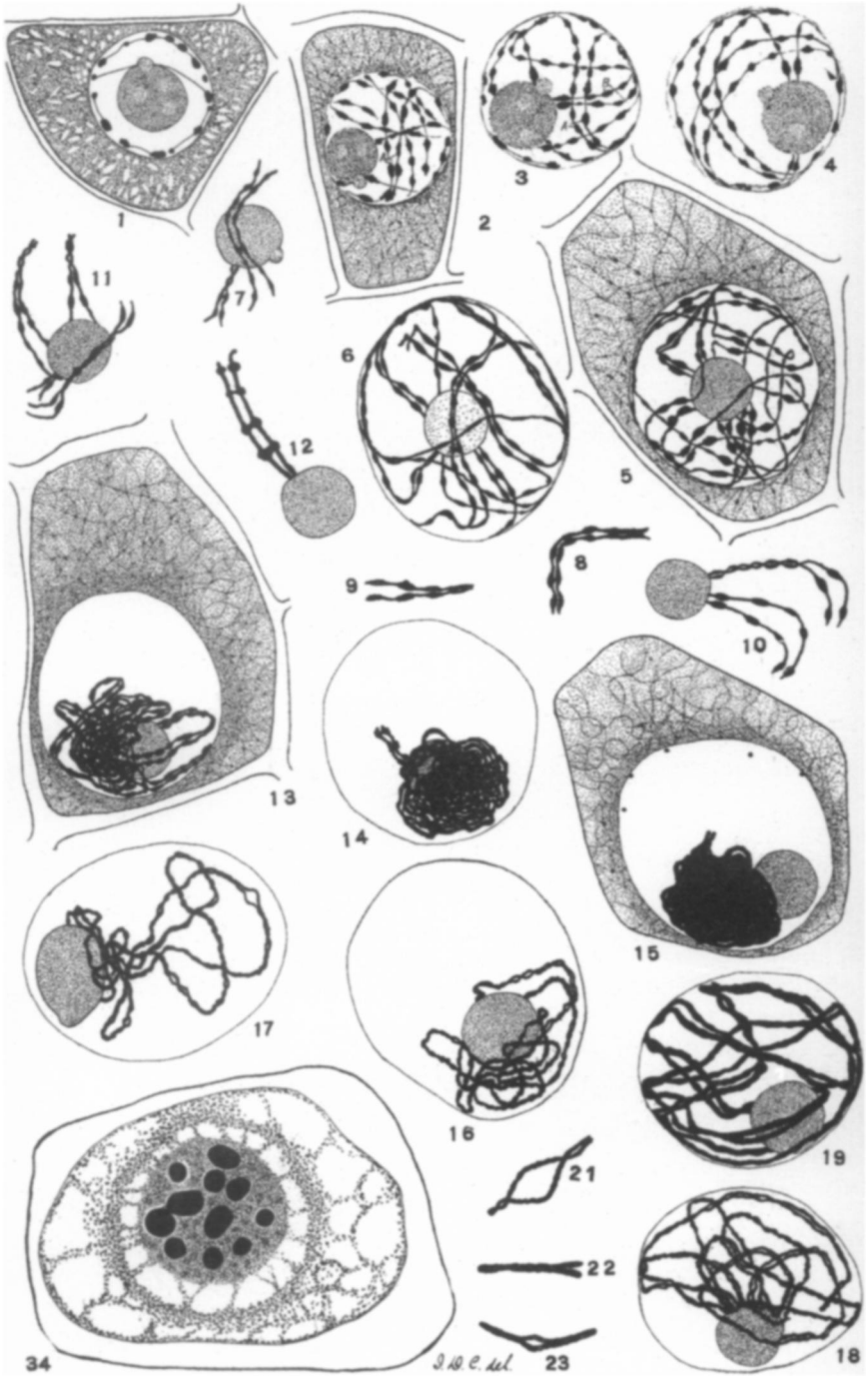
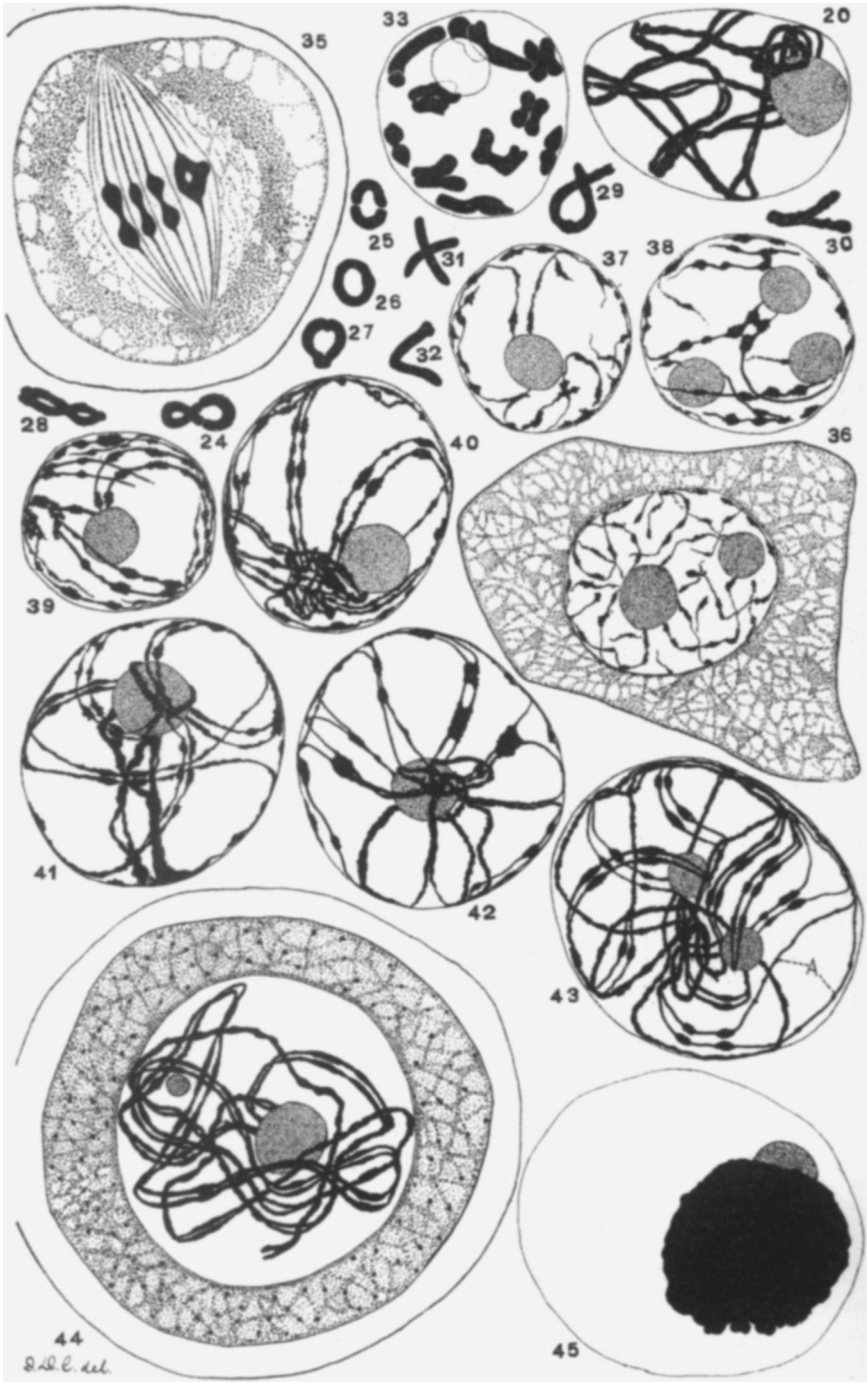
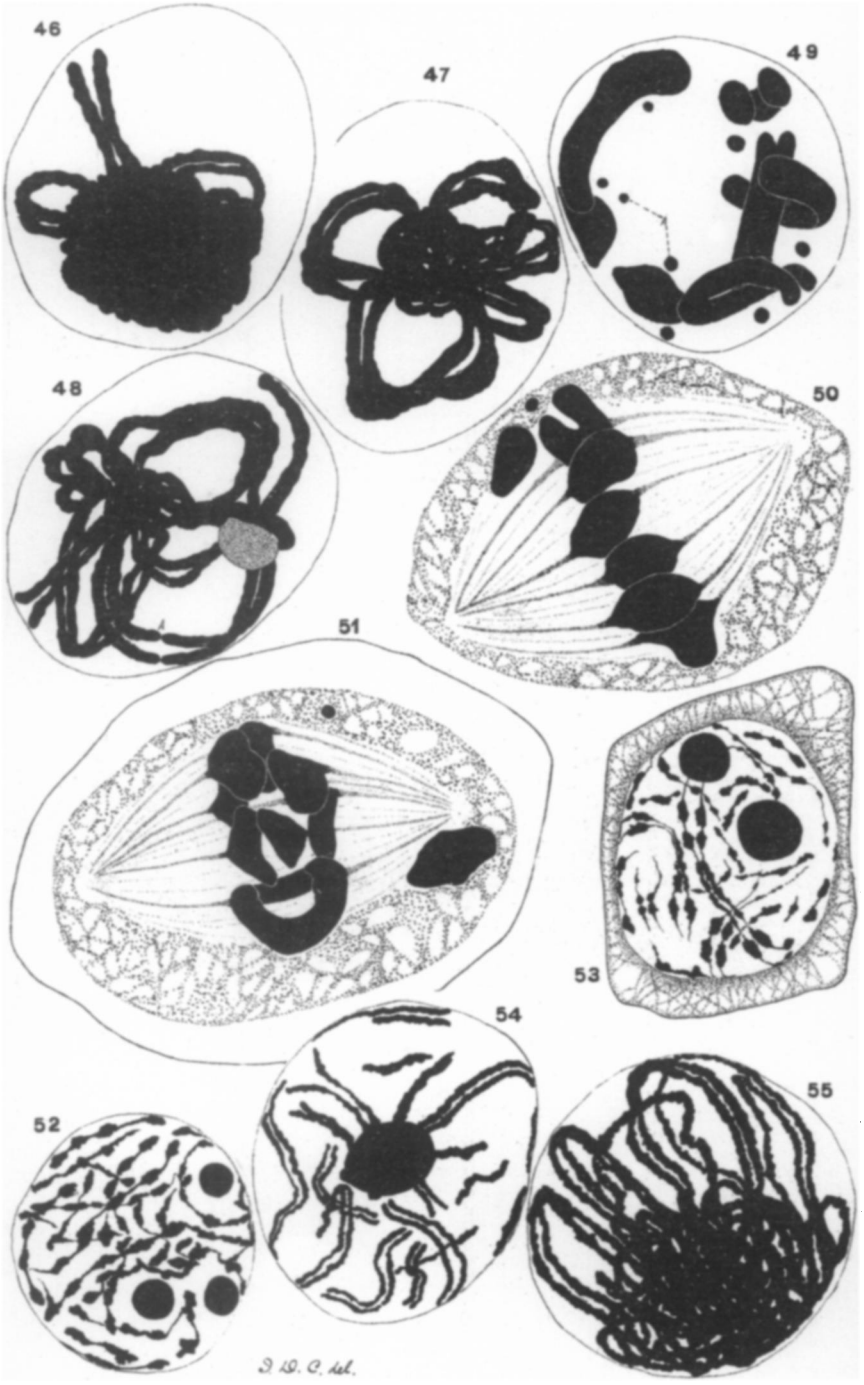
*These text-figures are inserted to illustrate the differentiation into linin and chromatin in the presynaptic threads, a character which the plates failed to show.



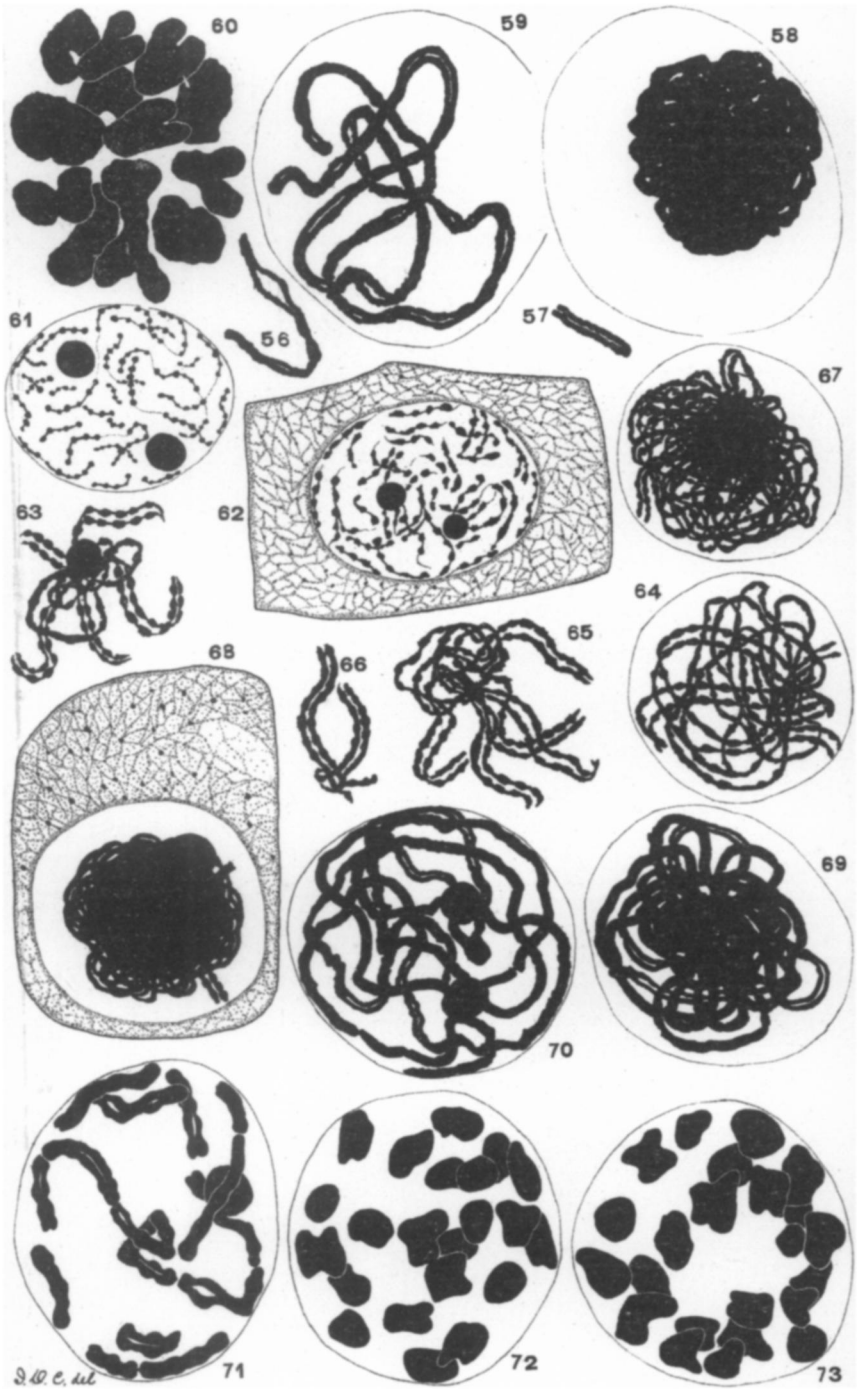
SYNAPSIS AND REDUCTION IN ACER



SYNAPSIS AND REDUCTION IN ACER AND SALOMONIA



SYNAPSIS AND REDUCTION IN SALOMONIA AND GINKGO



SYNAPSIS AND REDUCTION IN GINKGO AND BOTRYCHIUM

FIGURE 33. Prophase of first division; eleven chromosomes most of which show bivalent character.

FIGURE 34. Pole view of early metaphase of first division; different sized chromosomes.

FIGURE 35. Equatorial view of metaphase of first division; only part of chromosomes represented.

SALOMONIA BIFLORA

FIGURE 36. Early mother-cell; chromatin threads just forming.

FIGURE 37. Section of early mother-cell nucleus; formation of threads and arrangement near nuclear wall.

FIGURES 38 and 39. Sections of early presynaptic nuclei; beginning of parallel arrangement of threads.

FIGURE 40. Section of presynaptic nucleus; chromomeres increasing in size and activity; parallel threads.

FIGURES 41 and 42. Presynaptic nucleus, chromomeres beginning to fuse.

FIGURE 43. Nucleus just previous to beginning of contraction of chromatin thread into knot; threads nearly all show paired character; chromomeres smaller when threads are apart as at *a*.

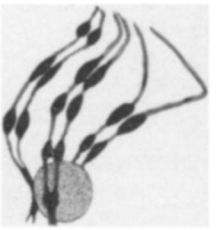


FIGURE 43

FIGURE 44. Mother-cell just previous to synapsis; threads contracting to form knot; cell rounded off; cytoplasm showing many deeply staining granules.

FIGURE 45. Synapsis.

FIGURE 46. Synapsis with portions of threads projecting from side of knot showing bivalent character.

FIGURE 47. Postsynaptic nucleus.

FIGURE 48. Postsynaptic nucleus; beginning of transverse division, *a*.

FIGURE 49. Prophase of first division; seven chromosomes; smaller bodies, *a*, probably a disorganizing nucleolus.

FIGURE 50. Metaphase of first division; heterotropic chromosome at one pole.

GINKGO BILOBA

FIGURE 52. Early mother-cell; beginning of formation of threads; several nucleoli.

FIGURE 53. Section of early mother-cell; beginning of parallel arrangement of chromatin threads; small amount of cytoplasm.

FIGURE 54. Section of presynaptic nucleus; threads thickening; parts of pairs moving closer together.

FIGURE 55. Nucleus just previous to synapsis; projecting threads showing pairing.

FIGURES 56 and 57. Portions of threads cut from periphery of close synaptic knots showing bivalent character.

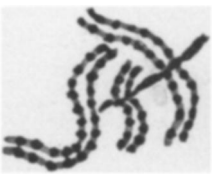


FIGURE 54

FIGURE 58. Nucleus in synapsis.

FIGURE 59. Portions of nucleus as the thread is disentangling from synaptic knot; bivalent character shown in places.

FIGURE 60. Late prophase of first division; twelve chromosomes; nearly all chromosomes showing bivalent character.

BOTRYCHIUM OBLIQUUM

FIGURE 61. Very early archesporial cell; chromatic material in the form of small granules and slender discontinuous threads.

FIGURE 62. Early mother-cell; chromatin beginning to form continuous threads; pairing of threads apparent in places.

FIGURE 63. Portion of chromatin from presynaptic nucleus; chromomeres still quite distinct; pairing evident.

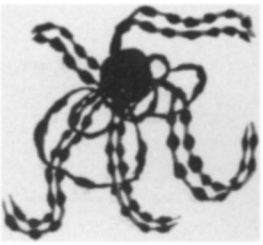


FIGURE 63

FIGURE 64. Section of nucleus previous to synapsis; chromomeres losing their identity.

FIGURE 65. Portion of nucleus a little later than figure 64.

FIGURE 66. Threads from knot just previous to synapsis.

FIGURE 67. Entire nucleus just previous to synapsis, moieties in most cases having united.

FIGURE 68. Mother-cell in synapsis.

FIGURE 69. Threads disentangling from knot; bivalent character shown in places; threads homogeneous throughout.

FIGURE 70. Loose postsynaptic spireme; beginning of transverse division.

FIGURE 71. Formation, by transverse division, of heterotypic chromosomes; many chromosomes showing bivalent character.

FIGURES 72 and 73. Prophase of first division; thick heterotypic chromosomes; several show undoubted bivalent character.